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Combining ability and heterosis as influenced by male-sterility inducing cytoplasm in sorghum [*Sorghum bicolor* (L.) Moench]

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Abstract An investigation was carried out to assess the efficiency of A₂ cytoplasmic-nuclear male-sterility (CMS) system in comparison to the widely used A₁ cytoplasm in terms of general combining ability (*gca*) effects of male-sterile (A-) lines and mean performance, specific combining ability (*sca*) effects and mid-parent heterosis of hybrids for days to 50% flowering, plant height and grain yield at International Crops Research Institute for the Semi-Arid Tropics, Patancheru, Andhra Pradesh, India in 2001 and 2002 rainy seasons. The material for the study consisted of six pairs of iso-nuclear, allo-plasmic (A₁ and A₂) A-lines and 36 iso-nuclear hybrids produced by crossing these A-lines with three dual restorer (R-) lines. The results revealed that cytoplasm and its first-order interaction with year, R- and A-lines did not appear to contribute to variation in iso-nuclear hybrids for plant height and grain yield. Cytoplasm had limited effect on *gca* effects of A-lines and on *sca* effects and mid-parent heterosis of iso-nuclear hybrids for days to 50% flowering, plant height and grain yield. The mean days to 50% flowering, plant height and grain yield of A₂

cytoplasm-based hybrids were comparable with those of widely used A₁ cytoplasm-based hybrids. The relative frequency of the occurrence of the A₁- and A₂-based hybrids with significant *sca* effects and mid-parent heterosis indicated that A₂ CMS system is as efficient as A₁ with a slight edge over A₁ for commercial exploitation. The implications of these results are discussed in relation to opportunities for broadening not only cytoplasm base but also nuclear genetic base of both the hybrid parents.

Keywords Sorghum · Cytoplasmic-nuclear male-sterility · Iso-nuclear · Allo-plasmic · Combining ability · Heterosis

Introduction

Sorghum [*Sorghum bicolor* (L.) Moench] is the fifth important crop after wheat, maize, rice and barley and is widely cultivated in the semi-arid regions of the world. Hybrid cultivar development in sorghum has been possible due to the discovery of workable cytoplasmic-nuclear male-sterility (CMS) (Stephens and Holland 1954) designated as A₁. Large numbers of CMS-based hybrids have been developed and released/marketed in countries with a well developed seed industry including India and China. The increased sorghum productivity in China (by >2 t ha⁻¹) and

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India (by $>0.5 \text{ t ha}^{-1}$) has been largely attributed to the adoption of hybrids (Deb et al. 2004). The commercial hybrids produced so far all over the globe are based on A_1 CMS system. However, based on the experience in other crops, the chances of these A_1 cytoplasm-based hybrids becoming vulnerable to unforeseen insect pests and/or diseases outbreak cannot be ruled out. For instance, outbreak of corn leaf blight disease in 1970 devastated the corn hybrids possessing Texas (T) cytoplasm (Tatum 1971). In addition to cytoplasm uniformity in the hybrids, use of single cytoplasm restricts nuclear genetic diversity of male-sterile (A-) as well as restorer (R-) lines. Therefore, to prevent such eventualities and to broaden the genetic base, the need for diversification of CMS base of sorghum hybrids was felt long back and as a result, several non-*milo* CMS systems were identified and developed (Schertz 1994) for use in hybrid breeding programs. However, utilization of these non-*milo* CMS systems at commercial level depends on factors such as stability of male-sterility, restorer gene frequency in the germplasm, effect of male-sterility inducing cytoplasm on agronomic traits, and the availability of commercially viable heterosis (Reddy et al. 2005).

The A_2 system, originally reported in IS 12662C (SC 171) line, from *Caudatum Nigricans* group belonging to subseries *caffra* (Schertz and Ritchey 1978) is stable and sufficient number of restorers are available on this cytoplasm (Reddy et al. 2005). However, its measurable effects on A-lines for their general combining ability (*gca*) effects and on specific combining ability (*sca*) effects and expression of heterosis of the hybrids is not clearly established, although such studies are important in CMS-based hybrid breeding programs. In pursuit of exploitation of alternate cytoplasm(s) for accomplishing the required diversification, agronomic performance of CMS-based hybrids cannot be compromised. Therefore, before large-scale exploitation of A_2 cytoplasm for hybrid cultivar development, it should be at least comparable, if not superior to the currently used A_1 cytoplasm. The results on the cytoplasmic effects in the past studies (Kishan and Borikar 1988; Maves and Atkins 1988; Secrist and Atkins 1989) are not only inconsistent, but

also the test hybrids based on alternate CMS systems in sorghum were not in common nuclear genetic background. Therefore, it is possible that the variable cytoplasm effects observed in such studies might be confounded with nuclear genetic differences. To discern the effect of different CMS systems on *gca* effects of A-lines and mean performance, *sca* effects and heterosis of hybrids, they must be in iso-nuclear background. While such studies on cytoplasm effects on mean performance of A-lines and hybrids involving iso-nuclear but allo-plasmic A-lines and common R-lines are limited in sorghum (Williams-Alanis and Rodriguez-Herrera 1992; Rodriguez-Herrera et al. 1993; Williams-Alanis et al. 1993; Moran and Rooney 2003), studies on the role of cytoplasm on *gca* effects of A-lines and on *sca* effects and heterosis of hybrids in sorghum are lacking. The assessment of *gca* effects of hybrid parents is important to judge their suitability for developing hybrids, as the mean performance of parental lines need not always be a good indicator of their *gca* effects. Further, the studies on the effects of cytoplasm on hybrid mean performance for various traits are although useful, as reported by Moran and Rooney (2003), *sca* effects of iso-nuclear hybrids would be more revealing since they reflect differential interaction of cytoplasm with nuclear genes of A-lines as well as R-lines and it is this interaction in higher magnitude and favorable direction that results in superior hybrid performance with commercially viable levels of heterosis.

In the present study, the effects of A_2 cytoplasm in comparison to A_1 on mean performance, combining ability and heterosis for agronomic traits were assessed using iso-nuclear, allo-plasmic A-lines and hybrids derived by crossing these A-lines with perfect dual R-lines.

Materials and methods

The materials for the study consisted of six iso-nuclear allo-plasmic (A_1 and A_2) A-lines in six different nuclear genetic backgrounds—ICSA 17, ICSA 37, ICSA 38, ICSA 42, ICSA 88001 and ICSA 88005 and three dual R-lines—ICSR 92003, ICSR 93001 and ICSR 93031. These were

developed at ICRISAT, Patancheru, India in a program to diversify the CMS-base of hybrid seed parents. While the six A-lines used in the study were originally developed in A₁ cytoplasm from improved germplasm crosses derivatives during 1980–1990 (Reddy et al. 2005), the dual R-lines were developed through either direct landrace selection or through their cross derivatives during early 1990s. These A-lines have been used for the production of commercial hybrid sorghums. The A₂ versions of the six A-lines were developed through repeated back crossing of A₁ maintainer (B-) lines to known A₂ cytoplasm source. The A-lines represent wide range of variation for days to 50% flowering (66–73 days), plant height (1.2–1.9 m) and grain yield potential (2.5–4.0 t ha⁻¹) (Table 1). Similarly, the R-lines are also diverse for days to 50% flowering (67–75 days), plant height (1.8–3.1 m) and grain yield potential (2.8–4.9 t ha⁻¹) (Table 1). As the seed parents and restorers have diverse geographical (India, USA, Sudan and Ethiopia) and racial (*durra*, *caudatum*, *guinea-caudatum* and *kafir-durra*) origins and represent wide variation for adaptive trait (days to 50% flowering), and yield potential, it was expected that they significantly differ for

combining ability and heterosis, considering strong association between mean performance of parents and their *gca* effects and their hybrid performance (Quinby and Karper 1946; Murty 1991, 1992; Bhavsar and Borikar 2002) and also strong association between parental diversity and hybrid superiority (Rao 1970; Shinde et al. 1983; Rana et al. 1985; Rana and Murty 1978).

The seed parents were crossed with the three dual R-lines in a line × tester mating design to produce 36 hybrid combinations in A₁ and A₂ CMS backgrounds. These hybrid combinations (hybrid trial) were evaluated in a split-split-plot design with three replications with R-lines in main plots, A-lines in sub plots and cytoplasm in sub-sub plots during 2001 and 2002 rainy seasons. The B-lines of the respective six A-lines and the three R-lines (parental trial) were evaluated in randomized complete block design with three replications in a contiguous block. In both hybrid and parental trials, each entry was planted in two rows of 4 m length with a spacing of 75 cm between rows and 10 cm between plants within a row at experimental fields of ICRISAT, Patancheru, India. All the recommended agronomic practices were followed to raise a healthy crop.

Table 1 Pedigree and agronomic characteristics of sorghum hybrid parents (A- and R-lines) used in developing hybrids

Hybrid parents	Pedigree	Days to 50% flowering	Plant height (m)	Grain yield (t ha ⁻¹)
A-lines				
ICSA/B 17	[(BTx 623 × 1807B) × B-lines bulk]-18-1-1	70	1.2	4.0
ICSA/B 37	[(BTx 623 × ((SC 108-3 × GPR 148)-18-4-1)) × B-lines bulk]-5-1-2-5	73	1.3	3.7
ICSA/B 38	[(BTx 623 × ((SC 108-3 × GPR 148)-18-4-1)) × B-lines bulk]-5-1-3-5	72	1.3	3.5
ICSA/B 42	[(BTx 623 × ((SC 108-3 × GPR 148)-18-4-1)) × B-lines bulk]-5-3-6-3	70	1.3	3.5
ICSA/B 88001	[(((BTx 623 × CSV 4) × B-lines bulk)-7-2-2) × Diallel 346-1) × Diallel 7-2-862]-1-1	66	1.9	4.0
ICSA/B 88005	[(((BTx 624 × UChV 2) × B-lines bulk)-5-1-1-1) × (((BTx 623 × UChV 2) × B-lines bulk)-10-1-4)) × DM 50]-1-1-1-1	66	1.4	2.5
Dual R-lines				
ICSR 92003	[(IS 23528 × (((IS 12622C × 555) × ((IS 3612C × 2219B)-5-1 × E 35-1))-5-2)) × PS 29154]-4-2-2-4	67	1.9	4.3
ICSR 93001	[(IS 23528 × (((IS 12622C × 555) × ((IS 3612C × 2219B)-5-1 × E 35-1))-5-2)) × PS 29159]-4-2-1-1	68	1.8	4.9
ICSR 93031	M 35-1-36	75	3.1	2.8

To ensure maximum expression, the crop was provided with protective irrigation. In both the experiments, the data on days to 50% flowering, plant height (m) and seed set (%) upon selfing and open pollination were recorded on five randomly selected plants in each entry and in each replication, while the data on grain yield were taken on whole-plot basis (border effects are assumed random/minimum) in both hybrid and parental trials.

Statistical analyses

The computed average values for days to 50% flowering, plant height and grain yield in both hybrid and parental trials were subjected to statistical analyses. The data on seed set (%) upon selfing and open pollination were not statistically analyzed as all the hybrids irrespective of cytoplasm background showed over 90% seed set and practically there was no variation in % seed set among the hybrids. The combined analysis of variance was carried out for days to 50% flowering, plant height and grain yield considering cytoplasm, A- and R-lines as fixed factors following split-split-plot design in hybrid trial. Considering that year-to-year variation predominantly stem from seasonal variation caused by changes in weather variables which are highly dynamic and not known in advance (Annicchiarico 2002), years were regarded as random factor. The homogeneity of error variances in the trials conducted in 2 years, as revealed by Bartlett's test (Bartlett 1937) provided statistical validity to carry out combined analysis of variance. Appropriate 'F' tests were conducted to test the significance of A-, R-lines, cytoplasm and their first- and second-order interactions at probability levels of 0.05 and 0.01.

Combining ability analysis was performed, separately for individual years using hybrid trial data according to Kempthorne (1957). Cytoplasm differences for *gca* effects of iso-nuclear A-lines and *sca* effects of iso-nuclear hybrids were tested using least significant difference calculated based on the standard error of mean for cytoplasm factor from the year-wise analysis of variance. The parental (B- and R-line) mean performance estimated from parental trial was used to

calculate mid-parent heterosis for days to 50% flowering, plant height and grain yield in individual years as:

$$\text{Mid - parent heterosis of a hybrid} = (\bar{A} - \bar{a})/\bar{a},$$

where, \bar{A} = mean performance of the hybrid in question; \bar{a} = mean performance of B-line of the respective A-line (mean performance of R-line divided by 2). The estimation of mid-parent heterosis requires hybrid and parental mean values, which were obtained from two different trials. The similarity of environmental effects in two different trials is essential for such a joint analysis. The homogeneity of error variances of hybrid and parental trials, as revealed by 'F' test ($P > 0.05$) provided statistical validity for the use of hybrid and parental mean values for the estimation of mid-parent heterosis. The performances of cytoplasm differences for mid-parent heterosis of iso-nuclear hybrids (considering A₁- and A₂-based hybrids as two groups) were tested using two-sample paired 't' test. All the statistical analyses were carried out using GENSTAT-5th edition package of Rothamsted Experiment Station, UK.

Results and discussion

Variances components

It follows from the combined analysis of variance (Table 2) that both A-lines (nuclear genotype) and R-lines are significantly different from each other for all the traits, justifying the selection of the hybrid parents (A- and R-lines) for the study. The temporal variation (years) did not seem to contribute to year \times cytoplasm, year \times R-line interactions for grain yield, despite highly significant mean squares due to years, which predominantly stem from seasonal variation caused by dynamic changes in weather variables from year to year (Annicchiarico 2002). However, seasonal changes over the years did have significant influence on the performance of A-lines over the years for grain yield as supported by significant mean squares due to year \times A-lines interaction. Thus, A-lines were

Table 2 Combined analysis of variance of sorghum iso-nuclear allo-plasmic male-sterile lines, their common restorers and hybrids, 2001 and 2002 rainy seasons, ICRISAT, Patancheru

Source of variation	df	Mean sum of squares		
		Days to 50% flowering	Plant height (m)	Grain yield (t ha ⁻¹)
Replication	2	2.23	0.07	0.20
Year	1	247.04**	1.08*	5.87*
Residual	4	2.25	0.09	0.80
R-line	2	123.63**	18.25**	34.17**
Year × R-line	2	2.89	0.21	3.58
Residual	8	10.37	0.05	1.33
A-line	5	97.38**	0.11**	1.29*
Year × A-line	5	5.95	0.01	2.40**
R-line × A-line	10	20.69**	0.05	2.96**
Year × R-line × A-line	10	8.77**	0.01	2.17**
Residual	60	2.75	0.02	0.52
Cytoplasm	1	8.56*	0.01	0.01
Year × cytoplasm	1	3.38	0.04	0.05
R-line × cytoplasm	2	3.19	0.01	0.35
A-line × cytoplasm	5	7.16**	0.01	0.49
Year × R-line × cytoplasm	2	6.89**	0.01	1.21
Year × A-line × cytoplasm	5	11.06**	0.02	1.05
R-line × A-line × cytoplasm	10	6.39**	0.02	0.66
Year × R-line × A-line × cytoplasm	10	10.85**	0.02	0.52
Residual	72	1.44	0.02	1.18

* Significant at $P = 0.05$ level** Significant at $P = 0.01$ level

more responsive to seasonal changes over the years than R-lines for grain yield.

The contribution of cytoplasm and their first-order interaction with A-line and second-order interaction with A-, R-line and year to the variation of iso-nuclear hybrids for days to 50% flowering was significant, suggesting significant overall influence of cytoplasm on the responses of hybrids for days to 50% flowering (Table 2). However, non-significant mean squares due to cytoplasm for plant height and grain yield indicated absence of cytoplasm effects on the expression of hybrids for these two traits. The absence of cytoplasm (A_1 and A_2) effects as well as their interaction with the environments for grain yield was also reported by Williams-Alanis and Rodriguez-Herrera (1994a).

The significant mean squares due to R-line × A-line interaction for days to 50% flowering and grain yield suggested significant variation of *sca* effects of hybrids and the *sca* effects are sensitive to seasonal changes over the years as indicated from significant mean squares due to year × R-line × A-line interaction.

Cytoplasm effects on *gca* effects

In hybrid breeding programs, the assessment of *gca* effects of different breeding lines is important to judge their suitability for developing hybrids, as mean performance of parental lines need not always be correlated with their *gca* effects. Also, *gca* effects reflect true genotypic value of a line, as these are estimated as mean effect of a line in a series of crosses. Thus, higher the *gca* of a line, higher is the average performance of its hybrids. Although in this study, most of the A-lines manifested significant *gca* effects for days to 50% flowering in both the cytoplasm (A_1 and A_2) backgrounds during both 2001 and 2002 rainy seasons, cytoplasm did not appear to have noticeable influence on *gca* effects, with significant cytoplasm difference detected only in one nuclear genetic background (ICSA 38) during 2001 rainy season (Table 3). Despite significant differences among A-lines for all the three traits (Table 2), *gca* effects of most A-lines within each of the cytoplasm were not significant for plant height and grain yield, suggesting that mean performance

Table 3 Estimates of *gca* effects of iso-nuclear sorghum A-lines as influenced by their cytoplasm, 2001 and 2002 rainy seasons, ICRISAT, Patancheru

A-lines	Days to 50% flowering				Plant height (m)				Grain yield (t ha ⁻¹)			
	2001		2002		2001		2002		2001		2002	
	A ₁	A ₂	A ₁	A ₂	A ₁	A ₂	A ₁	A ₂	A ₁	A ₂	A ₁	A ₂
ICSA 17	-0.94	0.07	0.04	-0.30	-0.06	-0.13**	-0.12**	-0.11*	0.27	-0.15	-0.53*	-0.23
ICSA 37	1.95**	2.39**	1.37**	2.37**	-0.02	0.02	0.01	0.04	0.02	0.05	0.37 ^a	-0.38
ICSA 38	1.62**	-0.16 ^a	1.93**	2.15**	-0.05	0.05	0.01	0.01	0.28	0.27	0.44	0.12
ICSA 42	-1.27* ^a	2.84**	0.26	-0.07	0.05	0.04	0.02	-0.04	-0.18	-0.68	-0.23	0.11
ICSA 88001	-0.49	-0.82	-1.63**	-1.52**	0.04	0.03	0.09*	0.06	-0.55	0.03	0.55*	0.50
ICSA 88005	-2.82**	-2.38**	-2.41**	-2.19**	-0.05	0.09* ^a	0.06	-0.03	0.29	0.35	-0.59*	-0.14
SE ± (gi)	0.53		0.44		0.05		0.04		0.36		0.26	
CD (A ₁ -A ₂) (<i>P</i> = 0.05)	1.49		1.22		0.13		0.12		1.00		0.74	

* Significant at *P* = 0.05 level** Significant at *P* = 0.01 level^a Significant cytoplasm differences

of A-lines need not always reflect their *gca* effects for these two traits. Significant cytoplasm differences were detected only in one nuclear genetic background for plant height (in ICSA 88005) during 2001 rainy season and for grain yield (in ICSA 37) during 2002 rainy season. However, the magnitude of these cytoplasm differences was small enough to have any practical significance. Thus, the study clearly showed that cytoplasm had limited influence on *gca* effects for all the traits investigated. It is important to note that the results of the present investigation apply only to the material used in the study, as A-lines are deliberate selections and the analysis is based on fixed-effects model. The absence of cytoplasm (A₁ and A₂) influence on *gca* effects for grain yield was also reported by Williams-Alanis and Rodriguez-Herrera (1994b).

Cytoplasm effects on hybrid mean performance

The results revealed absence of significant cytoplasm differences in hybrid mean performance for any of the traits under investigation during both 2001 and 2002 rainy seasons, except for days to 50% flowering during 2001 rainy season, when average performance of A₁- and A₂-based hybrids were examined (Table 4). However, when hybrid mean performance of individual allo-plasmic hybrids were examined, significant cytoplasm

effects were evident for all the traits, although no definite pattern of association of these traits with a particular cytoplasm was observed. For instance, the hybrids, ICSA 17 × ICSR 92003 (during 2001 and 2002 rainy seasons) and ICSA 42 × ICSR 93031 (during 2001 rainy season) in A₁ CMS background were significantly early by 2–3 days compared to those in A₂ background. On the contrary, the hybrids, ICSA 38 × ICSR 93031 and ICSA 88001 × ICSR 92003 (during 2001 and 2002 rainy seasons) and ICSA 42 × ICSR 93031 (during 2002 rainy season) in A₁ CMS background were significantly late by 1–2 days compared to those in A₂ CMS background. The differences in days to 50% flowering between A₁ and A₂ cytoplasm-based hybrids by 2–3 days are of little practical significance. These results are in conformity with those of Moran and Rooney (2003).

A₁ and A₂ cytoplasm-based hybrids had comparable grain yield potential when average of 36 hybrids was considered during both 2001 and 2002 rainy seasons. Secrist and Atkins (1989) also found similar grain yield potential of A₁ and A₂ cytoplasm-based hybrids. These results are not in conformity with some of the reports. For example, while Kishan and Borikar (1989) reported superiority of A₂ cytoplasm-based hybrids over A₁-based hybrids, Maves and Atkins (1988) observed lower grain yield potential of A₂ cytoplasm-based hybrids when compared to A₁-based

Table 4 Mean performance of iso-nuclear sorghum hybrids as influenced by male-sterility inducing cytoplasm of their A-lines, 2001 and 2002 rainy seasons, ICRISAT, Patancheru

Hybrid	Days to 50% flowering				Plant height (m)				Grain yield (t ha ⁻¹)			
	2001		2002		2001		2002		2001		2002	
	A ₁	A ₂	A ₁	A ₂	A ₁	A ₂	A ₁	A ₂	A ₁	A ₂	A ₁	A ₂
ICSA 17 × ICSR 93001	68	68	68	68	2.1	2.1	2.1	2.1	5.82	5.55	4.46	5.46 ^a
ICSA 17 × ICSR 92003	65 ^a	68	69	69	2.0	2.0	2.2	2.1	6.03	5.68	6.54	6.45
ICSA 17 × ICSR 93031	63	64	68	68	3.0	2.8	3.0	3.1	5.12	4.47	4.63	4.64
ICSA 37 × ICSR 93001	70	71	69 ^a	71	2.2	2.2	2.2	2.1	5.97	5.50	6.89 ^a	5.54
ICSA 37 × ICSR 92003	69	69	73	73	2.1	2.1	2.3	2.4	5.40	5.86	6.58	6.52
ICSA 37 × ICSR 93031	67	67	68	69	2.9	3.1	3.2	3.3	4.85	4.95	4.87 ^a	4.03
ICSA 38 × ICSR 93001	69	68	71	71	2.1	2.3	2.2	2.3	5.80	5.68	6.71	6.12
ICSA 38 × ICSR 92003	68	67	72	72	2.1	2.2	2.3	2.2	5.99	6.14	6.48	6.03
ICSA 38 × ICSR 93031	66	63 ^a	69	68	2.9	3.0	3.3	3.2	5.21	5.15	5.34	5.44
ICSA 42 × ICSR 93001	67	67	68	68	2.3	2.2	2.2	2.1	6.02	6.07	5.75	7.03 ^a
ICSA 42 × ICSR 92003	64	64	69	70	2.1	2.1	2.2	2.2	6.48	6.24	5.78	6.50
ICSA 42 × ICSR 93031	64 ^a	67	69	67 ^a	3.0	3.1	3.4 ^a	3.2	3.11	1.80	5.01 ^a	4.04
ICSA 88001 × ICSR 93001	66	68	66	66	2.3	2.3	2.3	2.2	4.73	6.14	6.56	6.81
ICSA 88001 × ICSR 92003	66	65 ^a	68	68	2.0	2.1	2.4	2.4	5.43	4.97	6.74 ^a	5.86
ICSA 88001 × ICSR 93031	65	64	66	67	3.1	3.0	3.3	3.2	4.35	5.15	5.56	6.04
ICSA 88005 × ICSR 93001	65	66	66	66	2.2	2.4	2.3	2.3	6.32	5.16	5.34	6.46 ^a
ICSA 88005 × ICSR 92003	63	64	69	70	2.1	2.3	2.3	2.4	4.98	6.26	5.69	5.56
ICSA 88005 × ICSR 93031	62	62	63	63	2.8	2.9	3.2	3.0 ^a	5.71	5.78	4.42	4.77
Mean	66 ^b	67	68	69	2.4	2.4	2.6	2.6	5.41	5.36	5.74	5.74
CD (A ₁ –A ₂) (<i>P</i> = 0.05) (at same levels A and R)	1.40		1.42		0.16		0.15		1.51		0.82	
CD (A ₁ –A ₂) (<i>P</i> = 0.05)	0.33		0.34		0.04		0.04		0.35		0.19	

^a Significant cytoplasm differences in an individual hybrids^b Significant cytoplasm differences over the average of all the hybrids

hybrids for grain yield. However, a perusal of pair-wise hybrids performance indicated significant cytoplasm differences for grain yield in a few nuclear genetic backgrounds. The hybrids such as ICSA 37 × ICSR 93001, ICSA 37 × ICSR 93031 and ICSA 42 × ICSR 93031 in A₁ CMS background were significantly superior to those in A₂ CMS background during 2002 rainy season. On the other hand, two A₂ CMS-based hybrids, ICSA 42 × ICSR 93001 and ICSA 88005 × ICSR 93001 were significantly superior to those based in A₁ CMS system. Lee et al. (1992) and Moran and Rooney (2003) have also reported absence of significant cytoplasm differences (between A₁ and A₃ and between A₁, A₂ and A₃ cytoplasm, respectively) for grain yield on the basis of average hybrids mean performance, but in pair-wise comparison of individual hybrids, significant cytoplasm differences were detected in three hybrids. Such differential trends in cytoplasm differences in some of the iso-nuclear hybrids

could be attributed to the interaction of cytoplasm with nuclear genes of A-lines and of R-lines in these hybrids. However, the distinction between cytoplasm effects and cytoplasm–nuclear interactions is complicated. This is not surprising considering that the very differentiation of CMS types is primarily based on the interaction of genes present on mitochondrial DNA and the corresponding nuclear restorer genes.

Cytoplasm effects on *sca* effects

Although, studies on the effects of cytoplasm on hybrid mean performance for various traits are useful, *sca* effects of iso-nuclear hybrids would be more revealing since they reflect differential interaction of cytoplasm with nuclear genes of A-lines as well as R-lines and it is this interaction in higher magnitude and desired direction that results in superior hybrid performance. While earliness was regarded as desired direction for

days to 50% flowering, tall stature and higher magnitude for plant height and grain yield, respectively, were considered as desired directions. Specific combinations of A- and R-lines with good *sca* effects will remain the essential requirements for the production of superior hybrids (Duvick 1999). In the present study, though, most of both A₁- and A₂-based hybrids showed significant *sca* effects for days to 50% flowering during 2001 rainy season, cytoplasm differences were absent in majority of the hybrids displaying significant *sca* effects (Table 5). Significant cytoplasm differences for *sca* effects for days to 50% flowering were evident only in three nuclear genetic backgrounds, ICSA 42 × ICSR 93001, ICSA 42 × ICSR 92003 and ICSA 42 × ICSR 93031, although there was no definite

pattern of association with a particular cytoplasm was observed. For example, while the hybrid ICSA 42 × ICSR 93001 in A₁ background showed significant *sca* effect toward lateness, the same hybrid in A₂ background showed significant *sca* effects toward earliness during 2001 rainy season. Another hybrid, ICSA 42 × ICSR 92003 in both A₁ and A₂ backgrounds manifested significant *sca* effects toward earliness during 2001 rainy season with significant cytoplasm differences during 2001 rainy season. During 2002 rainy season, only a few hybrids manifested significant *sca* effects for days to 50% flowering within each of the cytoplasm backgrounds. However, cytoplasm differences were absent during 2002 rainy season.

None of the hybrids (except ICSA 88005 × ICSR 93031 within A₂ cytoplasm during

Table 5 Estimates of *sca* effects of iso-nuclear sorghum hybrids as influenced by male-sterility inducing cytoplasm of their A-lines, 2001 and 2002 rainy seasons, ICRISAT, Patancheru

Hybrid	Days to 50% flowering				Plant height (m)				Grain yield (t ha ⁻¹)			
	2001		2002		2001		2002		2001		2002	
	A ₁	A ₂	A ₁	A ₂	A ₁	A ₂	A ₁	A ₂	A ₁	A ₂	A ₁	A ₂
ICSA 17 × ICSR 93001	0.85**	0.19*	-0.48	0.19	-0.09	-0.01	-0.01	0.04 ^a	-0.18	-0.03	-1.11	-0.41
ICSA 17 × ICSR 92003	0.24**	1.57**	-0.76	-1.09	-0.02	0.06	0.062 ^a	-0.05	-0.03	0.04	0.84	0.44
ICSA 17 × ICSR 93031	-1.09**	-1.76**	1.24	0.91	0.11	-0.04	-0.05	0.01 ^a	0.21	-0.02	0.26	-0.35
ICSA 37 × ICSR 93001	-0.04	0.52**	-0.48	0.52	0.01	-0.07	-0.02 ^a	-0.13	-0.22	-0.28	0.42	-0.18
ICSA 37 × ICSR 92003	0.69**	0.57**	1.24	0.24	0.01	-0.03	0.00	0.11 ^a	-0.41	0.02	-0.02	0.67
ICSA 37 × ICSR 93031	-0.65**	-1.09**	-0.76	-0.76	-0.02	0.10	0.02	0.03	0.19	0.26	-0.40	-0.49
ICSA 38 × ICSR 93001	-0.04	0.41**	0.63	0.74	-0.03	-0.01	-0.05	0.09 ^a	-0.21	-0.32	0.18	-0.10
ICSA 38 × ICSR 92003	0.69**	1.46**	-0.31	0.13	0.02	0.04	-0.01 ^a	-0.12	-0.08	0.08	-0.19	-0.32
ICSA 38 × ICSR 93031	-0.65**	-1.87**	-0.31	-0.87	0.01	-0.03	0.05	0.02	0.29	0.24	0.01	0.42
ICSA 42 × ICSR 93001	0.85**	-3.26** ^a	-0.37	-0.04	0.02	-0.04	-0.06	-0.02	0.47	1.02	-0.12	0.82
ICSA 42 × ICSR 92003	-0.76**	-5.20** ^a	-1.65*	-0.31	-0.03	-0.05	-0.08	-0.02 ^a	0.87	1.13	-0.22	0.16
ICSA 42 × ICSR 93031	-0.09 ^a	8.46**	2.02**	0.35	0.01	0.09	0.14 ^a	0.04	-1.35*	-2.15**	0.34 ^a	-0.98*
ICSA 88001 × ICSR 93001	-0.93**	0.74**	-0.48	-0.59	0.05	0.03	0.01	-0.02	-0.45	0.38	-0.08	0.22
ICSA 88001 × ICSR 92003	0.80**	-0.54**	-0.43	-0.54	-0.13	0.00	-0.02	0.05 ^a	0.19	-0.85	-0.04	-0.86
ICSA 88001 × ICSR 93031	0.13	-0.20*	0.91	1.13	0.08	-0.02	0.01	-0.03	0.26	0.48	0.12	0.64
ICSA 88005 × ICSR 93001	0.41**	0.30**	0.30	0.07	0.07	0.07	0.08	0.09	0.30	-0.92	-0.16	0.51
ICSA 88005 × ICSR 92003	0.13	0.35**	1.69*	1.80*	0.07	0.07	-0.02	0.84 ^a	-1.09	0.12	0.05	-0.52
ICSA 88005 × ICSR 93031	-0.54**	-0.65**	-1.98**	-1.87*	-0.11	-0.14	-0.06 ^a	-0.18*	0.79	0.79	0.11	0.01
SE ± (Sij)	0.09		0.75		0.08		0.08		0.62		0.46	
CD (A ₁ -A ₂) (P = 0.05)	2.59		2.12		0.22		0.04		1.73		1.28	

* Significant at *P* = 0.05 level

** Significant at *P* = 0.01 level

^a Significant cytoplasm differences

2002 rainy season) expressed significant *sca* effects for plant height within each of the cytoplasm backgrounds during both 2001 and 2002 rainy seasons. Significant cytoplasm differences were detected in ICSA 88005 \times ICSR 93031 during 2002 rainy season. Though significant cytoplasm differences were detected in four other nuclear genetic backgrounds, the differences do not assume importance, in view of the absence of significant *sca* effects of the hybrids within each of the cytoplasms for plant height during 2002 rainy season. Most of the hybrids in both A_1 and A_2 backgrounds failed to exhibit significant *sca* effects for grain yield. Significant cytoplasm differences were noticed in the only hybrid, ICSA 42 \times ICSR 93031 during 2002 rainy season, which showed significant *sca* effects for grain yield in both A_1 and A_2 CMS backgrounds during 2001 rainy season and in A_2 CMS background during 2002 rainy season. These results suggested limited influence of cytoplasm on *sca* effects for all the three traits under study. The absence of cytoplasm-dependent *sca* effects is also evident from the occurrence of more or less equal frequency of A_1 - and A_2 -based iso-nuclear hybrids that showed significant *sca* effects in desirable direction for plant height with a slight advantage of A_2 over A_1 for grain yield (Table 6). Williams-Alanis and Rodriguez-Herrera (1994b) also reported absence of cytoplasm effect on *sca* effects for grain yield.

Cytoplasm effects on heterosis

Even if the requirements of stability of CMS systems, availability of restorer genes in the germ-plasm and absence of adverse effects on economic traits are met, cytoplasmic effects on heterosis will ultimately determine the use of alternate CMS system for diversification of CMS-based hybrids. In general, mid-parent heterosis of A_1 - and A_2 -based hybrids did not appear to differ significantly for any of the traits, when mid-parent heterosis of all the A_1 -based hybrids, as a group was compared to all the A_2 -based hybrids as another group, as revealed by two-sample paired '*t*' test (Table 7). However, when individual hybrids were examined, cytoplasm differences were apparent for mid-parent heterosis for only grain yield, though no definite trend favoring any particular cytoplasm was observed.

Table 6 Frequency of iso-nuclear sorghum hybrids with significant *sca* effects and heterosis as influenced by male-sterility inducing cytoplasm of their A-lines, 2001 and 2002 rainy seasons, ICRISAT, Patancheru

Cytoplasm	Total no. of hybrids	No. of hybrids with significant <i>sca</i> effects and heterosis in desirable direction									
		Days to 50% flowering		Plant height (m)		Grain yield (t ha ⁻¹)					
		2001		2001		2001		2002		2002	
		<i>sca</i> effects	Heterosis	<i>sca</i> effects	Heterosis	<i>sca</i> effects	Heterosis	<i>sca</i> effects	Heterosis	<i>sca</i> effects	Heterosis
A_1	18	6	18	12	0	18	0	18	0	14	0
A_2	18	8	17	13	0	18	0	18	0	17	0

Table 7 Estimates of mid-parent heterosis of sorghum iso-nuclear hybrids as influenced by male-sterility inducing cytoplasm of their A-lines, 2001 and 2002 rainy seasons, ICRISAT, Patancheru

Hybrid	Days to 50% flowering				Plant height (m)				Grain yield (t ha ⁻¹)			
	2001		2002		2001		2002		2001		2002	
	A ₁	A ₂	A ₁	A ₂	A ₁	A ₂	A ₁	A ₂	A ₁	A ₂	A ₁	A ₂
ICSA 17 × ICSR 93001	-4.91**	-4.45*	-3.55**	-3.08*	28.54**	28.54**	39.38**	43.83**	57.94**	50.61*	13.61	39.19**
ICSA 17 × ICSR 92003	-5.17**	-5.17**	-3.49**	-4.41**	34.29**	30.41**	38.14**	31.95**	42.49**	43.67**	70.54**	68.06**
ICSA 17 × ICSR 93031	-7.11**	-3.78	-2.39	-3.33*	20.19**	20.19**	47.95**	51.22**	55.21**	46.20**	62.90**	63.12**
ICSA 37 × ICSR 93001	-8.79**	-9.26**	-3.49**	-0.70	19.60**	17.75**	45.53**	40.00**	46.44**	41.02**	56.44**	25.81**
ICSA 37 × ICSR 92003	-8.44**	-7.94**	-0.68	-0.68	51.90**	40.10**	40.80**	48.94**	73.56**	51.53*	52.56**	51.19**
ICSA 37 × ICSR 93031	-7.25**	11.12**	-5.14**	-3.74**	45.14**	49.15**	56.41**	58.06**	-10.89	-48.42*	46.47**	21.23*
ICSA 38 × ICSR 93001	-4.12*	-2.75	-0.23	0.23	31.34**	29.37**	36.89**	45.29**	58.99**	46.47**	49.29**	40.48**
ICSA 38 × ICSR 92003	-5.91**	-4.01*	-1.14	-0.23	22.15**	20.39**	33.99**	27.18**	23.98	60.94**	51.66**	41.22**
ICSA 38 × ICSR 93031	-4.40*	-3.94*	-2.82*	-3.30*	19.42**	19.42**	51.95**	50.37**	36.54*	48.17**	62.91**	65.99**
ICSA 42 × ICSR 93001	-4.79**	-7.17**	-3.08*	-3.08*	2.57**	8.47**	41.36**	39.14**	35.24*	23.79	25.28**	58.89**
ICSA 42 × ICSR 92003	-5.65**	-5.65**	-4.41**	-3.01*	42.02**	50.20**	33.99**	33.99**	60.60**	63.91**	33.39**	52.51**
ICSA 42 × ICSR 93031	-5.11**	-6.09**	-0.96	-3.81**	36.31**	31.11**	60.33**	52.38**	40.91	66.88**	49.89**	20.68**
ICSA 88001 × ICSR 93001	-5.03**	-6.85**	-4.10**	-4.10**	24.88**	31.73**	29.00**	25.24**	33.79*	31.03*	31.00**	35.90**
ICSA 88001 × ICSR 92003	-6.67**	-6.19**	-3.55**	-3.55**	27.6**	35.26**	23.51**	25.23**	76.04**	44.01*	36.90**	19.17**
ICSA 88001 × ICSR 93031	-5.31**	-6.7**	-3.40*	-2.91*	16.27**	22.80**	40.43**	37.57**	32.08*	35.39*	41.51**	53.70**
ICSA 88005 × ICSR 93001	-8.44**	-7.47**	-4.79**	-4.79**	16.33**	23.64**	52.19**	47.88**	31.66	65.44**	27.62**	54.35**
ICSA 88005 × ICSR 92003	-6.58**	-10.8**	-2.35	-1.87	39.76**	42.99**	39.99**	41.01**	44.72*	43.06*	33.92**	35.77**
ICSA 88005 × ICSR 93031	-8.82**	-8.34**	-9.39**	-8.91**	29.90**	36.99**	52.38**	42.86**	100.00**	102.45**	42.38**	53.61**
Two-sample <i>t</i> -test (paired) probability	0.40		0.47		0.21		0.33		0.79		0.88	

* Significant at $P = 0.05$ level** Significant at $P = 0.01$ level

For example, while the A₂-based hybrids such as ICSA 38 × ICSR 92003 and ICSA 42 × ICSR 93031 showed greater mid-parent heterosis for

grain yield than those based on A₁ cytoplasm, reverse was true in case of the hybrids such as ICSA 37 × ICSR 93001 and ICSA 88001 × ICSR 92003

during 2001 rainy season. Similarly, while a few A_2 -based hybrids such as ICSA 42 \times ICSR 93001, ICSA 42 \times ICSR 92003 and ICSA 88005 \times ICSR 93001 showed greater mid-parent heterosis for grain yield than those based on A_1 -based hybrids, reverse was true in case of the hybrids such as ICSA 37 \times ICSR 93001, ICSA 37 \times ICSR 93031 and ICSA 42 \times ICSR 93031 during 2002 rainy season. However, the magnitude and direction of mid-parent heterosis of A_1 - and A_2 -based hybrids were comparable for days to 50% flowering and plant height during both 2001 and 2002 rainy seasons. It was interesting to note that the frequency of heterotic hybrids for days to 50% flowering, plant height and grain yield in desirable direction in A_1 and A_2 cytoplasm backgrounds were more or less comparable with a slight edge in favor of A_2 for days to 50% flowering and grain yield (Table 6).

Thus, while there are significant cytoplasm effects on the expression in some of the nuclear genetic backgrounds of the hybrids, the magnitude of cytoplasm effects on *gca* effects of A-lines and on mean performance, *sca* effects and mid-parent heterosis of hybrids was small to have any practical significance. Further, magnitude of cytoplasm effects varied with the trait as well as with nuclear genetic backgrounds of A-lines and hybrid combinations depending on the interaction of cytoplasm with A- and R-lines, suggesting the need for assessing cytoplasm effects in diverse nuclear genetic backgrounds of A-lines as well as R-lines. The A_2 cytoplasm appeared to be slightly more advantageous as far as the frequency of hybrids with significant *sca* effects and mid-parent heterosis for days to 50% flowering and grain yield were concerned. The results have also demonstrated that the use of *gca* effects of A-lines and hybrids mean performance, *sca* effects and heterosis criteria are complementary and not exclusive ways of discerning cytoplasm differences. The simultaneous use of multiple criteria will always be advantageous in such a study. It may, however, be noted that the line \times tester analysis used in the study is on a fixed-effects model and the present results are applicable only to the material used in the study and some variation in the results might be observed if a different set of parents are evaluated.

Conclusions

The study, according to authors knowledge, is the first of its kind to assess the efficiency of A_2 CMS systems in comparison to the widely used A_1 system on all aspects of CMS-based sorghum hybrid cultivar development, i.e., cytoplasm effects on *gca* of A-lines and frequency of hybrids with high and significant *sca* effects and mid-parent heterosis using allo-plasmic, iso-nuclear A-lines and dual (A_1 and A_2) restorers. The results revealed that A_2 CMS system is comparable to the widely used A_1 system for plant height with a slight advantage of A_2 in favor of A_1 in terms of frequency of hybrids with significant *sca* effects and mid-parent heterosis for days to 50% flowering and grain yield. Thus, considering the restoration frequency, development of high yielding A-lines using A_1 restorers, and desirable *gca* effects of A-lines as well as mean performance, *sca* effects and heterosis of hybrids for economic traits such as grain yield, seed set (%) upon selfing and open pollination, days to 50% flowering and plant height, it is as advantageous to use A_2 CMS system as with A_1 CMS system among the alternate cytoplasms available. Moran and Rooney (2003) have also advocated A_2 CMS system as the best among the available alternative cytoplasms. However, A_2 CMS system is not popular as the anthers in A_2 male-sterile lines, unlike those of A_1 male-sterile lines mimic the fertile or maintainer lines and lead to difficulties in monitoring the purity of hybrid in commercial seed production. Such difficulties can be overcome through appropriate training to those involved in hybrid seed production. China has already developed and released A_2 cytoplasm-based hybrids for commercial cultivation (Shan et al. 2000). Extensive research is underway at ICRISAT, India and elsewhere for the development of A_2 cytoplasm-based hybrids.

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